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Skeletal Integrity of *Mimolagus rodens* (Lagomorpha, Mammalia)

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ABSTRACT

The postcranial skeleton of the Asian Paleogene species *Mimolagus rodens* was mistakenly described as that of a rodent and therefore not that of *Mimolagus*, a lagomorph. However, the foot structure confirms lagomorph affinity. The skull and skeleton are of a single individual.

INTRODUCTION

Bohlin (1951) published descriptions of two previously unknown fossil mammals from central Asia, *Mimolagus rodens* and *Anagalopsis kansuensis*. These were found in a Tertiary deposit in Kansu (Gansu), People's Republic of China, near Hui-hui-p'u on the river Po-yang-ho at approximately lat. 40°N, long. 98°E. *Mimolagus*, based on fragments of the skull, was believed by Bohlin to be a lagomorph. *Anagalopsis kansuensis* was based on a skull and lower jaw, a scapula, and several pedal elements. Although obviously related to the early Oligocene Asian genus *Anagale, Anagalopsis* could only be placed by Bohlin (1951) in the Mammalia, *incertae sedis*.

In the present paper we supplement Bohlin's descriptions and, consequently, reidentify certain "rodent" postcranial elements as those of the lagomorph *Mimolagus rodens*. These postcranial remains were actually found associated with the skull of *Mimolagus rodens* and were given the same field number (147), but nevertheless were considered by Bohlin to belong to some sort of rodent rather than to a lagomorph. He therefore discussed them in a separate section of his paper, although he obviously had lingering doubts because of the apparent association of the postcranial elements with the skull fragments upon which *Mimolagus rodens* was based (Bohlin, 1951, pp. 16, 27). The skeletal remains include various ankle and pedal elements, notably a complete astragalus.

Bohlin (1951) was unable to specify the age of the brick-red sandstone that produced the

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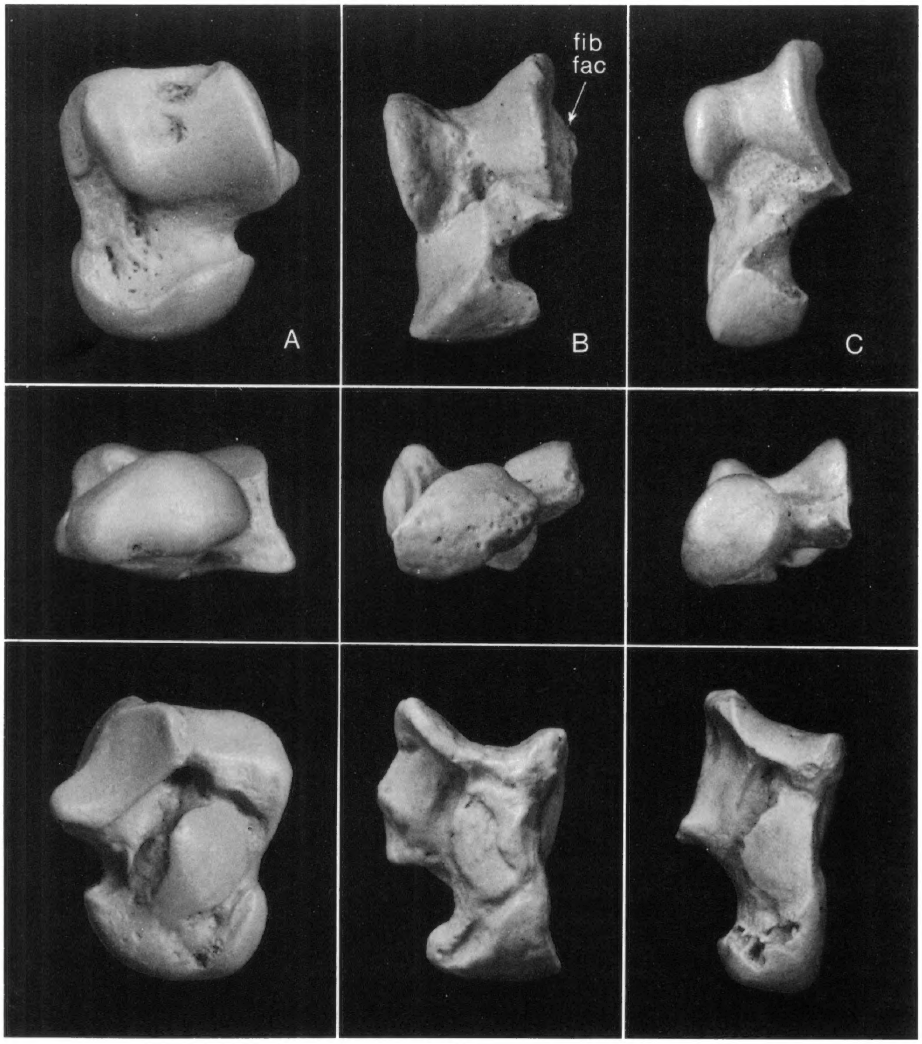

FIG. 1. Astragali of A, *Protungulatum* cf. *P. donnae* (MCZ Lot No. 18408, cast, reversed from left to right); B, *Mimolagus rodens* (IVPP No. RV51002.5, cast); and C, *Palaeolagus haydeni* (AMNH 6275, in part, cast). Dorsal (top row), anterior (middle row) and ventral (bottom row) views. Not to scale (see fig. 3). See text for description and explanation.

fossils he described. However, in an earlier paper (1940) he had noted that the unit lies above late Mesozoic sediments. Moreover, the unit "is unconformably overlaid by a heavy light brown series in which, however, only some fresh water gastropods have been found." Bohlin (1940, pp. 46, 47) believed that these deposits were disturbed by Pliocene folding. Clearly, the deposit containing *Mimolagus rodens* and *Anagalopsis kansuensis* is a Tertiary one, probably Paleogene in age because similar redbeds in the area are known to be of that age and because primitive ungulate postcranial remains were discovered at the same deposit (Bohlin, 1951, p. 46 and pl. 7, figs. 5, 6 where they are identified as questionably those of an artiodactyl). Fossil turtles were collected at the site as well (Bohlin, 1951, Introduction; 1953, p. 100), but as of 1953 these had not yet been studied. However, Yeh (1963) did briefly describe the reptilian material, referring it to a new genus

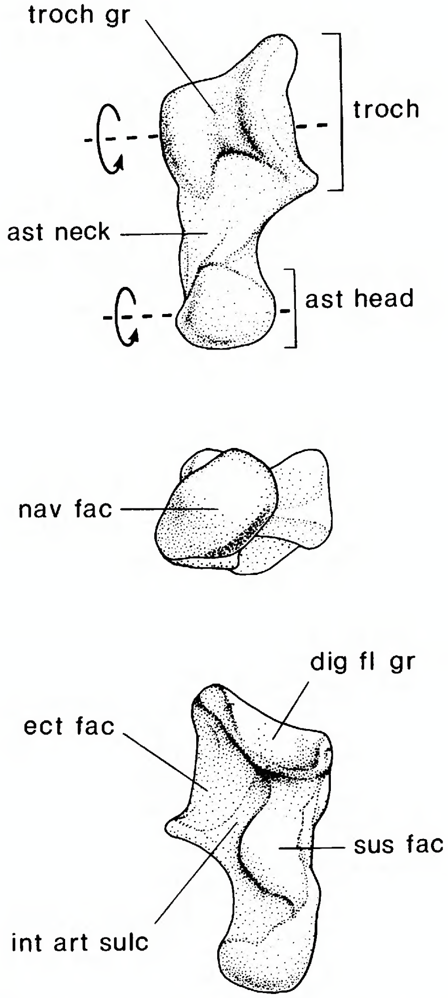

FIG. 2. Left astragalus of *Palaeolagus haydeni* (AMNH 6275, in part). Dorsal (top), anterior (middle) and ventral (bottom) views. *Abbreviations*: ect fac, ectal facet; sus fac, sustentacular facet; int art sulc, interarticular sulcus; ast head, astragalar head; ast neck, astragalar neck; nav fac, navicular facet; dig fl gr, digital flexor groove; troch gr, trochlear groove. From Bleefeld (MS). Terminology adapted from Cifelli (1983). Natural proportions shown in figure 3.

and species, *Kansuchelys chiayukanensis*, and assigning an Oligocene or late Eocene age to the deposit that produced it, *Mimolagus*, and *Anagalopsis*.

Li (1977, pp. 110, 117) tentatively erected a "Family Mimotonidae" for *Mimolagus*

FIG. 3. Astragali of (left to right) *Protungulatum* cf. *P. donnae, Mimolagus rodens* (cast) and *Palaeolagus haydeni,* showing natural proportions.

Bohlin, 1951, and *Mimotona* Li, 1977. He placed this "Family" in a new superfamily Eurymyloidea of the order Anagalida, but his "Family Mimotonidae" is not available according to Article 15 of the International Code of Zoological Nomenclature.

Abbreviations for institutions referred to in the text are as follows: AMNH, American Museum of Natural History, New York, New York; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, People's Republic of China; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

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SYSTEMATICS

CLASS MAMMALIA

ORDER LAGOMORPHA

MIMOLAGUS BOHLIN, 1951

MIMOLAGUS RODENS BOHLIN, 1951

TYPE: Not formally designated, but obviously the unnumbered skull whose fragments were discussed by Bohlin (1951). The specimen is now in the IVPP collections and bears the numbers RV51001.1 and RV51001.2. We formally designate it as the type specimen of the above species. The two skull fragments, which Bohlin was unable to fit together, comprise the snout and a right maxilla.

DESCRIPTION

The snout has long, tightly curved, gliriform incisors that Bohlin estimated to have extended backward to the level of the anteromost premolar of the continuous cheek tooth series, in the anterior part of the maxilla, following the now empty anteromost premolar alveolus, four well-worn cheek teeth are preserved; the last is broken away posteriorly. Bohlin believed that a fifth cheek tooth would have been present in life at the posterior end of the cheek tooth series. The maxilla also has two small openings behind those for the enlarged gliriform incisors; Bohlin interpreted these to have housed a second pair of incisors, a characteristic feature of all known lagomorphs.

The cheek teeth of the earliest lagomorphs are characteristically unilaterally hypsodont and transversely elongate. Bilateral hypsodonty was achieved in later members such as the North American Oligocene leporid, *Palaeolagus haydeni,* and all extant lagomorphs. Where unilateral hypsodonty occurs, however, the enamel base of the tooth is strongly oblique with respect to the occlusal surface of unworn teeth. This is a consequence of greater lingual lengthening (hypsodonty) of the tooth (Tobien, 1978). In *Mimolagus rodens,* the upper cheek teeth are transversely elongate. While it can be seen that upper molars of *Mimolagus* are very worn, the enamel base lies nearly parallel to the crown surface. Possibly unworn teeth of *Mimolagus* would display at least moderate obliquity of the enamel base.

In unworn teeth of early lagomorphs, the occlusal topography is complicated by an internal invasion of enamel which creates a series of valleys and ridges. In *Hsuiannania,* one of the earliest recognized lagomorphs (McKenna, 1982), the occlusal surface of the upper molars has two distinct buccal cusps (paracone and metacone), with a deep basin of enamel between them. Later lagomorphs possess a lingual invasion of enamel called a hypostria, which spans the tooth from the lingual to the buccal edge in advanced forms. The upper molars of the type specimen of *Mimolagus rodens* are too worn to reveal anteroposterior lobes, but the first two maxillary teeth (the last premolar and M^1) preserve remnants of the buccal cusps seen in *Hsuiannania* and mid-Tertiary lagomorphs.

Bohlin's detailed analysis of the microstructure of the incisor enamel of *Mimolagus* does not falsify relationship to lagomorphs. There are multiprismatic, inclined lamellae as in lagomorphs (probably the primitive condition [L. J. Flynn, personal commun.]), and a buccal layer of enamel is poorly differentiated in *Mimolagus.* Lagomorphs have one layer of enamel and rodents have two, but which is advanced is not certain. In any case, the details of lagomorph enamel microstructure are not comparable to that of any studied rodent.

A pair of nasal bones is also preserved, lying dorsomedial to a groove that apparently housed a long rearward projection of the premaxilla.

Based on more recent work (Szalay, 1977; McKenna, 1982; Bleefeld, MS), we concur with Bohlin's (1951) taxonomic assignment of the cranial and part of the postcranial material of *Mimolagus rodens* to the Lagomorpha. Although his descriptions of that material are complete, we supplement them with a revised analysis of the associated astragalus IVPP no. RV51002.5. Lateral compression of the astragalar body is strong, and articulation surfaces are sharply delineated. A stable articulation with the tibia is created by a deep, well-defined trochlear groove. Parallel axes of rotation occur between the astragalar tibial trochlea and the astragalar navicular facet;

the major rotational axes of both lie in the sagittal plane, roughly parallel to the long axis of the astragalus (see fig. 2). The astragalar neck is slightly medial to the tibial trochlea and the bone preserves a small fibular facet (fig. 1). A striking feature is the rather broad, triangular shaped extension of the navicular facet onto the dorsal aspect of the astragalar neck. The broad ectal facet is largely vertically oriented (fig. 1).

Bleefeld (MS) has presented an analysis of lagomorph phylogeny based primarily on characters of the pes. In particular, the lagomorph astragalus is laterally compressed, and there are sharp delineations between articular surfaces. The navicular facet lies in the sagittal plane and its axis of rotation is parallel to that of the astragalar tibial trochlea (fig. 1). It is curious that Bohlin (1951) referred the astragalus to Rodentia, *incertae sedis,* while including a statement that "the rotational plane of the astragalonavicular articulation evidently was approximately parallel to that of the tibioastragalar articulation." In more advanced lagomorphs (*Palaeolagus, Oryctolagus*), the astragalar fibular facet is lost, although it is retained by the Paleocene lagomorph *Pseudictops.* In all known lagomorphs the navicular facet extends onto the dorsal surface of the astragalar neck, increasing the area for navicular articulation. The "rodent" astragalus figured by Bohlin agrees with this description in all details. The calcaneus referred to the Lagomorpha by Bohlin (IVPP no. RV51102.4) bears two major medial articular surfaces: the calcanear sustentacular facet, and one proximodistally oriented facet on the anteromedial wall of the bone. These occur in all known lagomorphs, and serve as articular surfaces for the astragalus. Moreover, the astragalus referred to here, IVPP no. RV1002.5, articulates medially with Bohlin's lagomorph calcaneus (leaving exposed a large calcanear fibular facet) at each of those surfaces. These are diagnostically lagomorph features (Szalay, 1977; Bleefeld, MS) and offer no evidence of any close relationship to rodents. We therefore conclude that the calcaneus and Bohlin's "rodent" astragalus are of the same individual, and we refer the astragalus to *Mimolagus rodens,* with whose type specimen the astragalus and other postcranial remains were associated in the field.

Mimolagus rodens is indeed a lagomorph.

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